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Inferring topology from dynamics in spatial networks

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Abstract We examine dynamics of oscillating populations in habitats described as networks of connected patches where the connections are not regular. This system would be typically analysed focusing either on the population dynamics, or measuring dispersal directly or indirectly. We focus on the question of the degree to which the dynamical patterns, as reflected in synchrony, reveal the underlying dispersal pathways. This would represent a bridge between two major spatial approaches, topological and dynamical. We show how local populations can be synchronized even if there is no direct dispersal route between them, while the stepping-stone populations are not synchronized. This leads to the surprising result that the topological structure of the underlying network is not reflected simply in patterns of synchrony across space in population dynamics. This shows that, with our current tools, the complex relationship between the underlying dispersal patterns and population dynamics prevent us from determining network structure through the observation of population dynamics.

Keywords metapopulation dynamics · modularity · synchronization · functional connectivity

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1 Introduction

Spatial networks describe functional relationships between habitat patches linked by processes such as dispersal or gene flow [Hanski and Gilpin(1997), Urban and Keitt(2001), Fortuna et al(2009), Albert et al(2013)]. Determining to what degree the topological structure of the network depicting how links are distributed across patches affects the biological processes that occur in that network is a long-standing question [Holland and Hastings(2008), Gilarranz and Bascompte(2012)]. The inverse problem, of determining the network describing actual dispersal routes also becomes very important, for example in the design of effective reserves.

From a conservation point of view, connectivity has been increasingly identified as an important feature affecting long term persistence [Hastings and Botsford(2006), Crooks and Sanjayan(2006)]. In some cases, the direct observation of network structure may be appropriate using either direct observation of movement, genetic techniques, simulation of physical processes like ocean currents, or other indirect approaches [Swearer et al(1999), Nathan(2006), Jordano et al(2007), Siegel et al(2008), Fortuna et al(2009)]. In other cases, only observations of dynamics on local populations may be appropriate or available. For example, there has been substantial interest in examining patterns of synchrony over space in a variety of organisms [Bjørnstad et al(1999a), Liebhold et al(2004)]. Recently, [Powney et al(2011)] related landscape suitability with synchrony to estimate landscape's functional connectivity. However, these investigations of synchrony have typically not focused on the role of network structure, with the exception of [Holland and Hastings(2008)]. The question of whether we can infer the dispersal pathways from synchronous populations remains open.

Given the importance of connectivity and its influence on dynamics, we suggest investigating further the relationship between connectivity and dynamics. From a methodological point of view, topological approaches have used network theory to unravel structural properties such as the presence of modules, that is, groups of nodes that interact more strongly among themselves than with other nodes in the network [Guimerà and Amaral(2005),Fortuna et al(2009)]. Dynamical approaches such as [Holland and Hastings(2008)], on the other hand, have identified clusters as sets of nodes displaying synchronous dynamics [Kaneko(1998)]. In this paper we ask: To what degree are these two approaches—topological and dynamic—coincident? Namely, are the modules identified through topological measures similar to the clusters of synchronized populations? An affirmative answer would provide a new tool for unravelling connectivity. Indeed, if all patches from a module were showing synchronous dynamics, it would be enough to record the dynamics of a patch from each topological module to know the temporal dynamics of all patches in the landscape. A negative answer, on the other hand, would help determine the important features of connectivity for biological dynamics.

2 Methods

We simulate the dynamics of a metapopulation on a modular spatial network. Then, we extract a dynamically inferred network where two patches are linked if their dynamics are significantly synchronized. Afterwards, we compare the clusters from the dynamical approach and the modules of the spatial network. We develop a similarity measure to quantify the coincidence of the topological and dynamical approaches. We compare our results with a null model in order to assess their statistical significance.

2.1 Spatial network

We create a spatial network composed of one hundred habitat patches linked through dispersal with a modular spatial structure (Fig. 1a). To ensure that the network is highly modular, we create four small random networks with a Poisson degree distribution [Erdős and Rényi(1959)], and then we randomly establish links between patches from different modules.

To detect modules on the spatial network we used the algorithm introduced by [Guimerà and Amaral(2005)]. This algorithm maximizes modularity through simulating annealing [Kirkpatrick et al(1983)]. For binary, undirected networks, the modularity function is given by:

$$M = \sum_{s=1}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right], \quad (1)$$

where N_M is the number of modules, L is the number of links in the network, l_s is the number of links between nodes in module s , and d_s is the sum of the degrees of the nodes in module s . Different outputs of the module identification algorithm can find slightly different partitions of the network. Nevertheless, for the spatial networks used in this paper, the algorithm always found the exact same modules.

2.2 Metapopulation dynamics

To introduce a dynamic explicit model running on the network of patches, we simulate a metapopulation model where local dynamics were described by the Ricker model for a single species [Ricker(1954)]. Local populations are linked through dispersal. To implement the Ricker model, we assume two phases, dispersal and

growth. The variation in population density during the dispersal phase is determined by the dispersal rate D , defined as the fraction of individuals leaving their patch to uniformly disperse into adjacent patches. Therefore, every adjacent patch receives a number of individuals from patch i that is equal to DN_i/k_i , k_i being the degree of patch i . The number of individuals in patch i after the dispersal phase ($\tilde{N}(i)$) is a balance between emigration and immigration. This can be written as:

$$\tilde{N}_t(i) = (1 - D)N_t(i) + D \sum_{j=1}^{k_i} \frac{N_t(j)}{k_j}, \quad (2)$$

where $N_t(i)$ is the density of the population at patch i before the dispersal phase, k_i is the number of neighbours of patch i , and $N_t(j)$ is the density of the population in the neighbouring patch j .

Next, the growth phase is defined by the Ricker model and can be written as:

$$N_{t+1}(i) = \tilde{N}_t(i)e^{r(1-\tilde{N}_t(i))}. \quad (3)$$

In equation (3), the population density is scaled by the carrying capacity. In order to introduce stochasticity, we slightly change the growth rate at every patch and at every time step. Specifically, we add or subtract to the growth rate a random value between zero and ten percent of the growth rate. We run the model 100 times for every value of growth rates. However, our results are insensitive to these small values of stochasticity. Moreover, given the universality properties of the Ricker model —as discussed in [Wysham and Hastings(2008)]— and other non-linear discrete maps that exhibit period doubling bifurcations [Stewart(1989), Schroeder(1991)], our results will likely be insensitive to the choice of the specific model.

2.3 Dynamically-inferred network

We extract a dynamically-inferred network [Eguíluz et al(2005)] from the recorded local dynamics. To determine whether a link exists between two patches, we calculate the Pearson correlation coefficient of the rates of change ($N_{t+1}(i)/N_t(i)$) between every two patches i and j . If the correlation is significantly positive ($p < 0.01$), these patches are linked. To assess the generality of our results, in the section 2 of the Online Resource we show that our results holds when two other measures of synchrony are used [Hanski and Woiwod(1993), Bjørnstad et al(1999b)], and they do not depend on the selected p-value. A dynamically-inferred cluster will contain any such nodes directly linked to one another, so that different clusters will contain different, unconnected subnetworks.

We look at both short-term dynamics—provided by the first one-hundred iterations—and long-term dynamics—provided by the last one thousand iterations—from a 10,000 iterations run. Since both short and long-term time scales produce equivalent results, hereafter we will be illustrating results for the long-term dynamics.

2.4 Absolute and relative similarity

After the above procedure, we have two spatial networks, a topological network based on distances between patches, and a dynamically-inferred network based on the synchrony between the rate of change of the population density of patches. Our aim is to compare both networks, and measure how similar they are. We measure the similarity S between two networks as follows:

$$S = 1 - \frac{X}{L_s + L_d - C}, \quad (4)$$

where X is the number of links that have to be added or removed to make the networks identical, L_s is the number of links of the spatial network, L_d is the number of links of the dynamically-inferred network, and C is the number of common links between both networks. X is calculated by subtracting the adjacency matrix of the spatial network from the adjacency matrix of the dynamically-inferred network, and then counting the number of non-zero elements. Therefore, $S \in [0, 1]$. If there is a perfect one-to-one matching between the two networks, then $X = 0$, and therefore $S = 1$. If there would be no single link in common, $X = L_s + L_d$ and $C = 0$; therefore $S = 0$.

Equation (4) is an absolute measure of similarity. We want to discriminate whether the similarity value is larger than what it would be expected if the links of the dispersal network would be distributed randomly (see Online Resource section 4 for more details). For that we compared the observed value with a benchmark provided by a null model. The null model used randomizes the spatial network preserving the degree of each habitat patch [Maslov and Sneppen(2002)]. We produced 100 randomizations. In each of the randomized networks we then simulate population dynamics and obtain the dynamically inferred network. We then define relative similarity as the following z-score:

$$z = \frac{S - \bar{S}_r}{\sigma_r}, \quad (5)$$

where S is the observed similarity value between the real pair of topological and dynamical networks, and \bar{S}_r and σ_r are the average and standard deviation of similarities between the initial topological network and the dynamic network arising from the randomized network. If the z -value is above 1.96, the spatial network and the dynamically-inferred network are significantly similar. We can

therefore explore to what degree similarity depends on growth rate and dispersal rate.

3 Results

The number and size of dynamic clusters, and the number of links between patches from dynamically-inferred clusters, indicate the amount of synchrony through the landscape. Figures 1b and c show the structure of the dynamically-inferred network for two different growth rates. Figure 1b illustrates a scenario of low growth rate where the dynamically-inferred network is divided in two large hyper-connected clusters. Figure 1c, on the other hand, shows several dynamic clusters, but most of those clusters are formed by one or a few patches, and are randomly distributed. These network layouts, where the coordinates of the patches are preserved, indicate how population synchrony is distributed across space. Figure 1 aims to illustrate the differences between the partition in modules between the topological network (Fig. 1a) and the dynamically-inferred network (Figs. 1 b and c). We show how dispersal relationships within a complex network can induce local populations to be synchronized even if there are no direct dispersal routes among them. As noted, there is little—if any—resemblance between both types of partition.

Next, to generalize the above results, we explore how similarity is influenced by model parameters, dispersal and growth rate. Figure 2 explores the influence of growth rate in the number of dynamic clusters, similarity, and relative similarity between dynamically-inferred and spatial networks. Absolute similarity decreases when the growth rate leads the dynamics towards a chaotic attractor (Fig. 2a). However, if we use relative similarity calculated as the z-score in equation 5, we find no significant differences between the similarity with the dynamically-inferred

network or with a randomized spatial network for any growth rate (Fig. 2b). Regarding the number of clusters, they first increase within the chaotic domain, decrease around the domain of the first periodic window, and peak again for higher growth values (Fig. 2c). It seems that the lower the number of dynamic clusters, the larger the absolute similarity.

Regarding the influence of dispersal rate on the measured properties, absolute similarity increases with dispersal (Fig. 3a) until reaching a maximum for a dispersal rate around 0.45, and then decreasing in a linear fashion. There is still no significant trend when measuring relative similarity (Fig. 3b). As expected, the number of dynamic clusters decreases with dispersal (Fig. 3c). A dispersal rate slightly higher than 0.2 is enough to create one single synchronized dynamic cluster.

To broadly study the combined effect of growth rate and dispersal, Figures 4a to 4c explore a wide range of parameter combinations. Figure 4a shows that the highest similarity occurs for high growth and dispersal rates. However, as shown before, there is no significant tendency in the relative similarity measure (Fig. 4b). For the number of dynamic clusters (Fig. 4c), most of the parameter space is governed by values lower than five. Nevertheless, for low growth rate and high dispersal rate, the landscape is desynchronized and a large number of dynamic cluster emerges.

4 Discussion

Our results suggest that there is apparently no correlation between the topological partition of a network in modules and the resulting partition from the dynamically-derived network. This means that patterns of correlation among patches are dif-

1 difficult to assess from the information on the topology of the network alone. Since
 2 population synchronization is directly related to conservation issues (e.g., when
 3 assessing the risk of metapopulation extinction or the number of effective reserves
 4 to achieve some conservation goal), this means that information on the metapop-
 5 ulation dynamics is important to complement topological approaches.

6 The changes in the number of clusters and absolute similarity with growth
 7 rates reported here are, to some extent, expected given previous work on the role of
 8 chaotic dynamics in spatial synchronization. For example, [Rasmussen and Bohr(1987)]
 9 demonstrated that near the onset of chaos, the following relationship between
 10 the largest Lyapunov exponent (λ) and the spatial coherence length (ξ) holds:
 11 $\xi \approx \lambda^{-1}$. The more chaotic a system is, the faster the spatial correlation decays
 12 with distance. Far away patches tend to oscillate independently of each other.
 13 From the point of view of metapopulation dynamics, this means that “ups” and
 14 “downs” can be compensated and that globally, the metapopulation may be very
 15 stable. Ironically, it is the local instability, which generates this global stability
 16 [Solé et al(1992)]. However, this previous work was based on regular lattices. Here
 17 we describe how this overall trend is modulated in more heterogeneous landscapes.

18 The identification of modules—also called communities—in complex networks
 19 has received a lot of attention in the recent years [Girvan and Newman(2002),
 20 Guimerà and Amaral(2005), Rozenfeld et al(2008), Fortuna et al(2009)]. Modular food
 21 webs were suggested to be more robust to perturbations [May(1972)], which has
 22 been recently confirmed with realistic food-web models and appropriate mea-
 23 sures of modularity [Stouffer and Bascompte(2011)]. Specifically, modules buffer
 24 the spread of perturbations such as the extinction of a species across the entire
 25 network. Regarding spatial networks, our work suggests that topological mod-
 26 ularity does not necessarily map into synchronous population groups. However,

even in this scenario, the flow of individuals between patches is largely affected by the modular structure of the network. As we show in the section 1 of the Online Resources, individuals move preferentially within—rather than between—modules. The explanation of how that dynamic effect is not reflected by patch dynamics is intriguing. One sees that two harmonic oscillators could be synchronized even if they are not directly connected to a synchronous patch. In fact, synchrony (locking at a phase difference of zero), is only one possible outcome of connection. Other phase differences (such as exactly out of phase, or π apart) may also be stable in systems of two coupled patches [Goldwyn and Hastings(2008), Goldwyn and Hastings(2009)]. Thus, the counter-intuitive result that there is a lack of correlation between dynamic and topological structures may have an underlying mathematical explanation. The synchronization of the hundred harmonic oscillators described by the Ricker’s model at each habitat patch seems therefore, unpredictable.

How to maintain the connectivity of fragmented landscapes continues to be a key question in the face of global change. Our results suggest that we may need to combine different approaches, i.e., dynamic and topologic, to successfully tackle this issue. Spatio-temporal networks can provide insight not only into demographic processes, but also into gene flow and the subsequent mapping of genetic variability [Dyer and Nason(2004), Rozenfeld et al(2008), Fortuna et al(2009)].

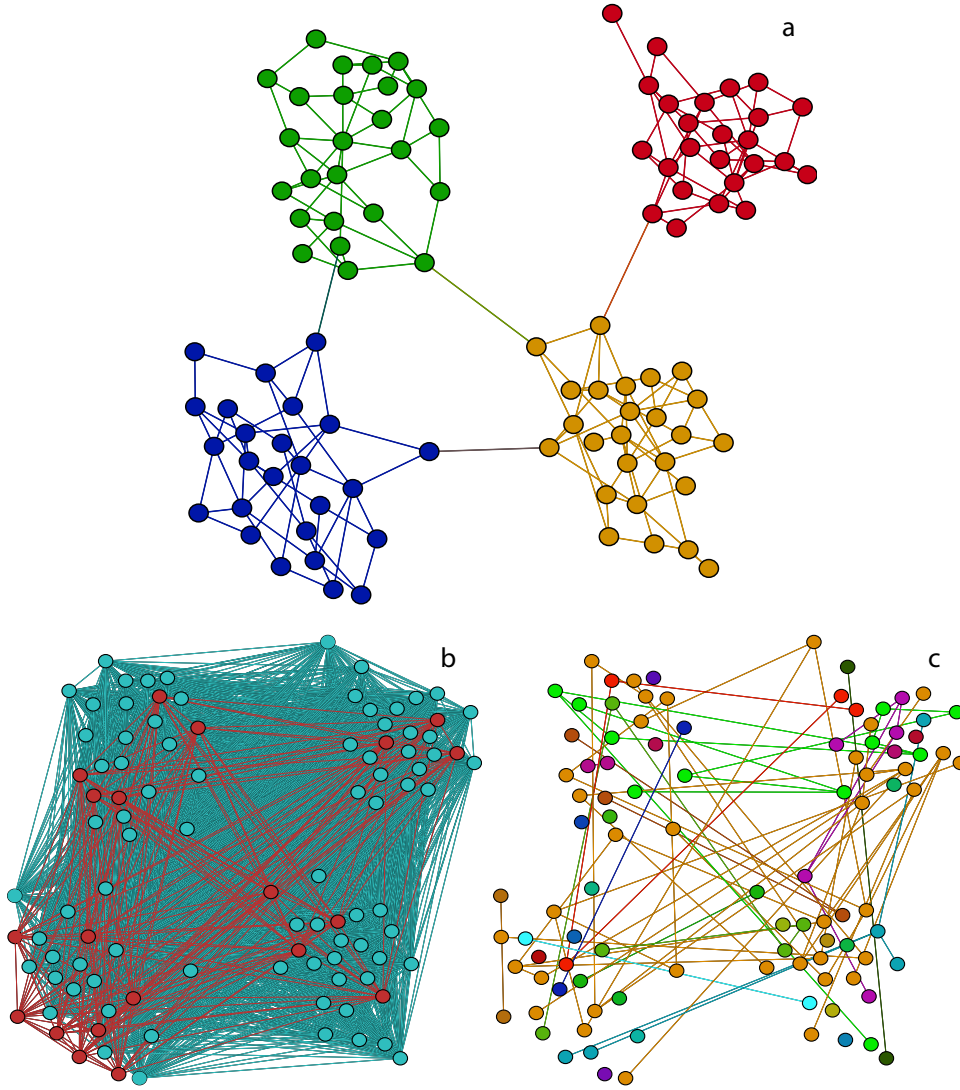


Fig. 1 Topological and dynamically-inferred networks. **a**, Spatial modular network with a Poisson degree distribution composed by 100 nodes. The color of a node identifies the module where it belongs. These modules have been found using the module-finding algorithm by Ref. [Guimerà and Amaral(2005)]. In this case, each module has 25 nodes. **b** and **c** represent a dynamic network, where the coordinates of nodes were taken from the layout of the spatial network, and two nodes are linked if their temporal correlation is significant. Each color represents a different dynamic cluster. The network in panel (b) has only 2 clusters, while the network in panel (c) has many clusters. Model parameters are $r = 2.25$ and $D = 0.01$ (b); and $r = 4$ and $D = 0.01$ (c).

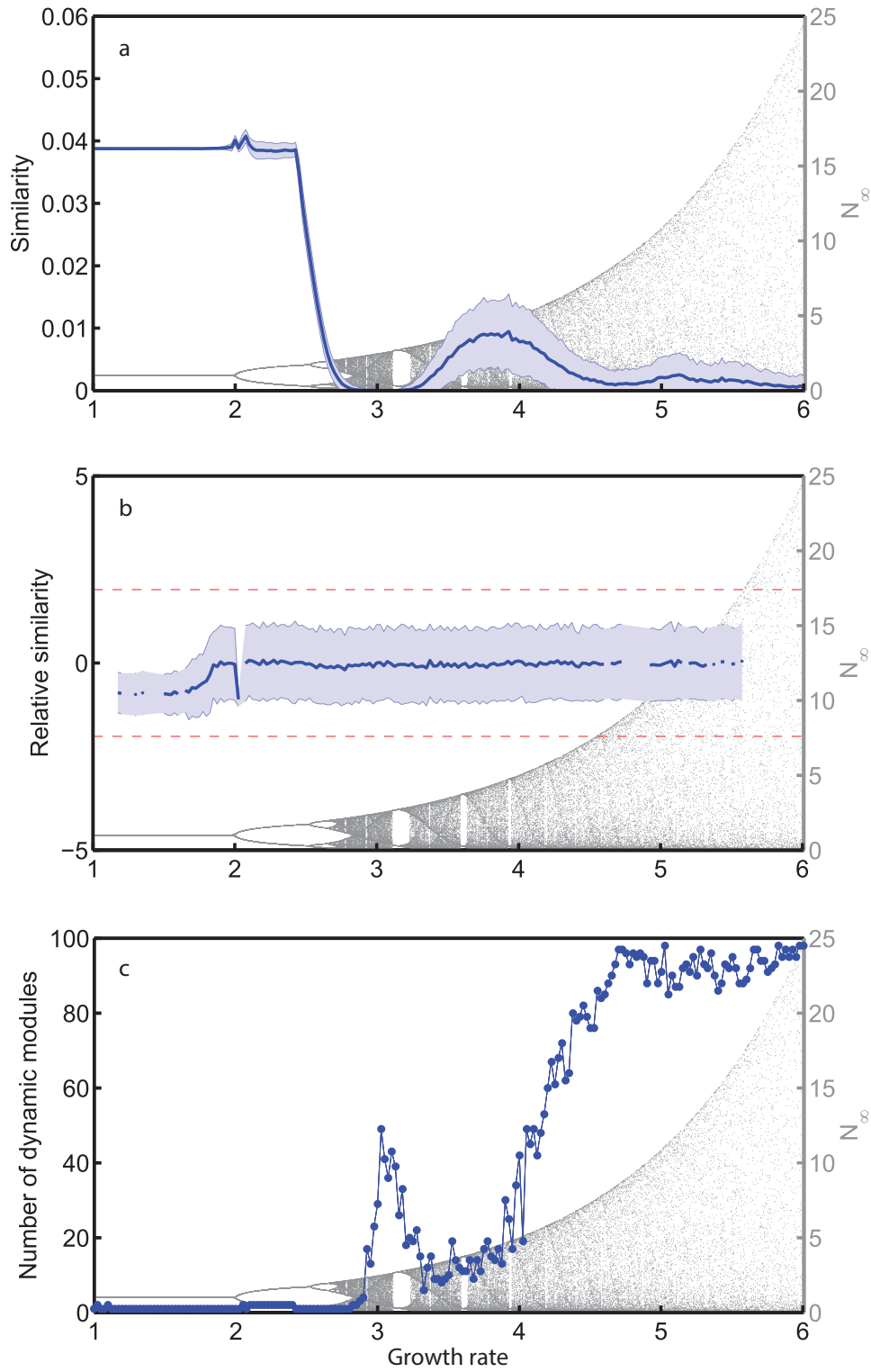


Fig. 2 As a function of the growth rate, here we represent: absolute (a) and relative (z-score; b) similarity between spatial and dynamic-inferred networks, and number of dynamic clusters (c). Dispersal rate is equal to 0.01. The Ricker's bifurcation diagram [May and Oster(1976)] is superimposed in the background. The shaded blue area represents the 95% confidence intervals, and the solid line indicates the 500 replicates' mean. Notice that for the number of dynamic modules, there is no variation across replicates.

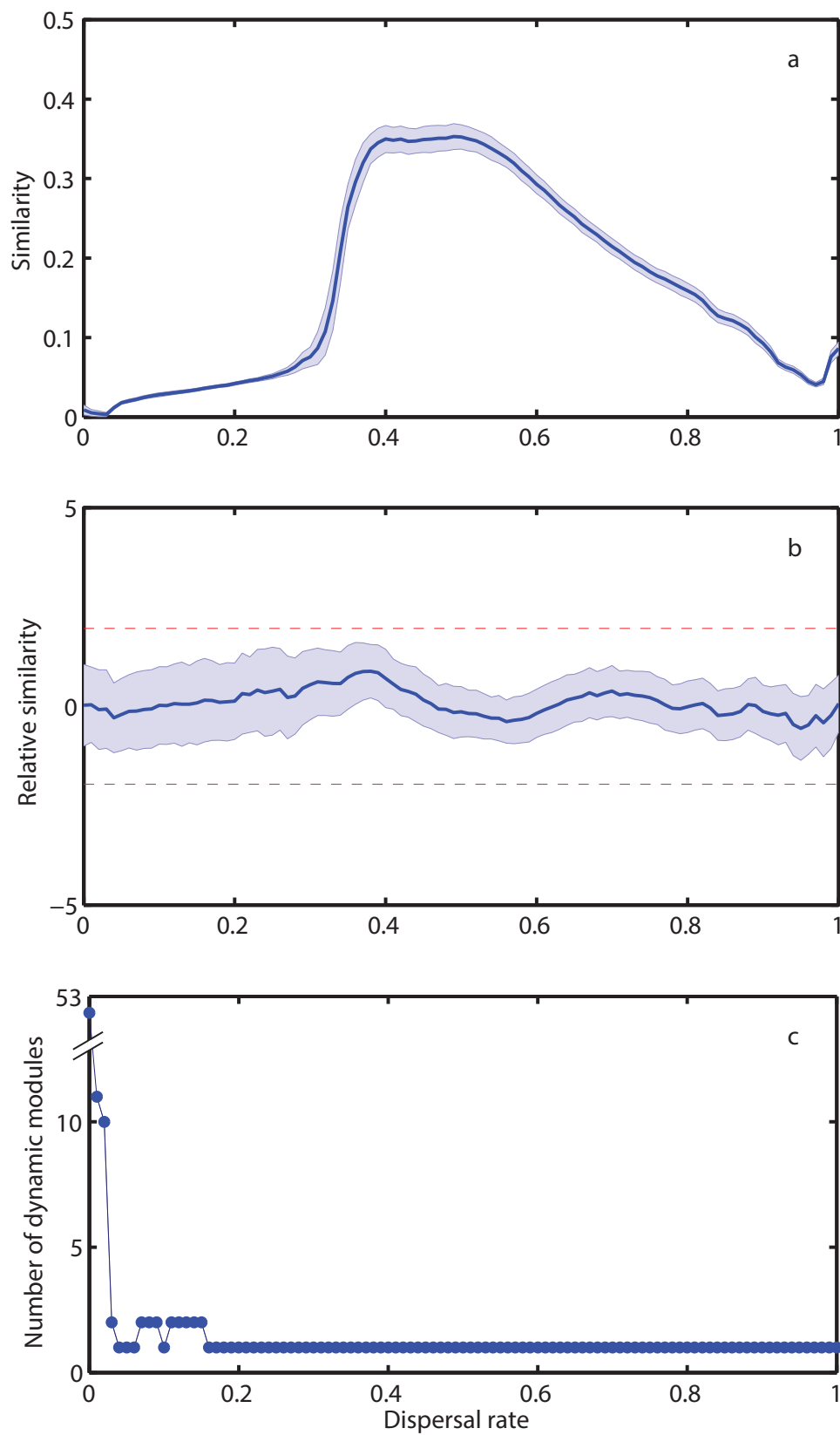


Fig. 3 As a function of the dispersal rate, here we represent: absolute (a) and relative (z-score; b) similarity between spatial and dynamic-inferred networks, and number of dynamic clusters (c). The growth rate is equal to 3.5. The shaded blue area represents the 95% confidence intervals, and the solid line indicates the 500 replicates' mean. Notice that for the number of dynamic modules there is no variation across replicates.

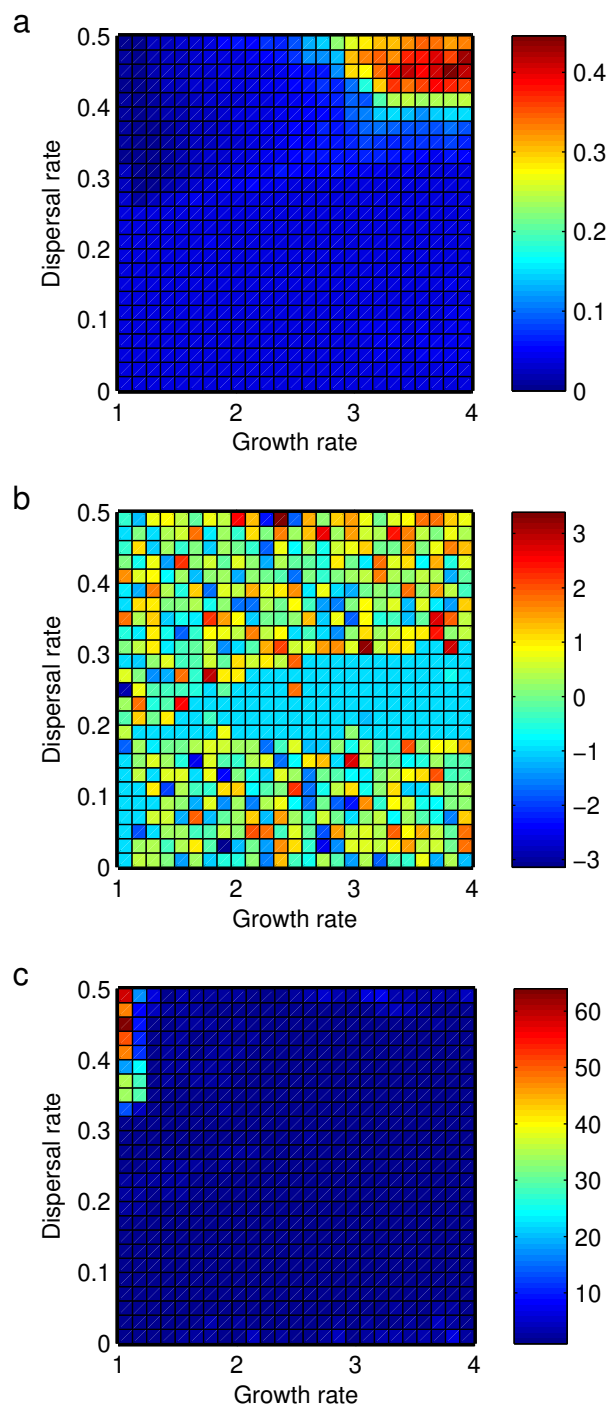


Fig. 4 For a wide range of combinations of dispersal and growth rates here we represent: absolute (**a**) and relative (z-score; **b**) similarity between spatial and dynamic-inferred networks, and number of dynamic clusters (**c**).

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